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ELECTROSENSORY FREQUENCY AND INTENSITY DISCRIMINATION IN THE WAVE-TYPE ELECTRIC FISH *EIGENMANNIA*

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Summary

Eigenmannia's frequency and intensity discrimination thresholds were determined for a range of seven frequencies (50–1700 Hz), centered on a fish's individual discharge frequency, using a conditioned go/no-go paradigm. The threshold criterion was '50 % correct choices' (of the rewarded stimulus, S+, over the unrewarded stimulus, S−); this was validated by testing for statistically significantly shorter response latencies for the S+ compared with the S− stimulus.

The stimuli consisted of sine wave bursts presented for up to 20 s, repeated at $2\,s^{-1}$ (rise and fall times of an individual burst, 50 ms; holding time, 250 ms; silence, 150 ms). When testing for frequency discrimination, the sine wave bursts alternated in frequency (Δf); for intensity discrimination, every other sine wave burst was of increased intensity (ΔI). The reference stimulus intensity was 30 dB with reference to a fish's individual absolute threshold for a continuous sine wave at that frequency, previously determined using a conditioned go response.

Sensory discrimination was best close to a fish's individual discharge frequency. At 30 dB sensation level, fish discriminated frequency differences as small as 0.52 Hz (0.60 and 0.79 Hz in two other individuals) and intensity differences as small as 0.56 dB (1 dB in two other fish).

At stimulus frequencies different from a fish's discharge frequency, *Eigenmannia*'s frequency discrimination declined at lower frequencies at a rate of up to $1\,Hz\,octave^{-1}$, and at higher frequencies at a rate of up to $3\,Hz\,octave^{-1}$. For *Eigenmannia*'s intensity discrimination a similar loss was observed: at frequencies lower than a fish's discharge frequency, intensity discrimination thresholds rose at a rate of less than $1\,dB\,octave^{-1}$, while the rate was below $2\,dB\,octave^{-1}$ for higher frequencies.

Compared with other acoustico-lateral senses in lower vertebrates, *Eigenmannia*'s electrosensory frequency and intensity discrimination is unusually high, in the range of that known for audition in the most sensitive higher vertebrates with a cochlea (for example, human). This emphasizes *Eigenmannia*'s specialized 'active' electrosensory system, which detects the presence of a stimulus field as the modulation of a fish's own 'carrier' signal in amplitude and phase (beat analysis),

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as opposed to 'passive' sensory systems, which must deal with unpredictable signals from the environment as they occur.

Introduction

The South American knife fish *Eigenmannia* displays a wave-like electric organ discharge (EOD), usually of constant frequency (250–600 Hz) and amplitude (usually below 100 mV_{p-p}, measured head-to-tail; Lissmann, 1958; Watanabe and Takeda, 1963; Hopkins, 1974; Kramer, 1985). Electroreceptors in the skin report about the animal's own and other electric signals (review, Zakon, 1988). The electrosensory-motor system is used for active object detection (see review by Bastian, 1986) and social communication (see reviews by Hagedorn, 1986; Kramer, 1990*a*,*b*).

It is unknown whether *Eigenmannia* can discriminate electric wave stimuli of different frequencies or intensities. *Eigenmannia* could selectively filter for its own species-specific frequency, being insensitive to other species' EOD frequencies, because of relatively sharp electroreceptor tuning to an individual fish's EOD frequency (other frequencies would be suppressed; Scheich *et al.* 1973; Hopkins, 1976; Hopkins and Heiligenberg, 1978). Knudsen's (1974) behavioral threshold curves for sine wave stimuli show that fish are most sensitive at their own EOD frequency, with the threshold rising rather steeply on both sides (6.5–18 dB $octave^{-1}$ on the 'low', 20 dB $octave^{-1}$ on the 'high' side). *Eigenmannia* could therefore be 'tone-deaf', that is, unable to discriminate different frequencies, if one of two conditions holds: (1) electroreceptor tuning curves are all similar, or (2) small differences in 'best' frequencies or filter slopes, if present, are not centrally represented.

However, other sensory and behavioral data support the opposite hypothesis of fine frequency and intensity discrimination. (1) *Eigenmannia* modulates its discharge frequency during social behavior; frequency increases, decreases and discharge arrests have all been observed (Hopkins, 1974; see reviews by Hagedorn, 1986; Kramer, 1990*a*,*b*). A well-known frequency modulation is the jamming avoidance response (JAR), an EOD frequency change often evoked by a stimulus sufficiently close in frequency to a fish's EOD frequency (Watanabe and Takeda, 1963; see reviews by Heiligenberg, 1988, 1989; Kramer, 1990*a*,*b*). (2) Adult males discharge in the lower, adult females in the upper, species-specific range (Hagedorn and Heiligenberg, 1985; Kramer, 1985). [However, for mate recognition, fish do not seem to rely on this frequency difference, but instead recognize the sexually dimorphic EOD waveform (Kramer and Zupanc, 1986; Kramer and Otto, 1988) by a time-domain mechanism (Kramer and Otto, 1991)]. (3) The perception of minute amplitude changes in *Eigenmannia*'s own EOD is the basis for active object detection (Lissmann, 1958; Heiligenberg, 1973).

With the observation that tuberous electroreceptor tuning curves are not all alike (see, for example, Viancour, 1979), and because central nervous mechanisms have only partially been identified (see review by Carr, 1990), the hypothesis of

good electrosensory discrimination in *Eigenmannia* cannot be dismissed *a priori*. A behavioral test is the only means to address adequately the questions of frequency and intensity discrimination in a complex sensory system like that of *Eigenmannia*.

Materials and methods

Three juvenile *Eigenmannia lineata* (10–14 cm) were used. They had not undergone any tests before. They were kept isolated in their experimental tanks (75 cm×42 cm×40 cm high; 27±1 °C; water conductivity, 100±3 μS cm^{-1}; L:D, 12:12 h; Fig. 1). A plastic mesh partition divided the aquarium into a 'home' and a 'stimulus' section (mesh size, 1.5 mm). A short ceramic tube (outer and inner diameters, 5 cm and 4.4 cm, respectively; length, 3 cm) sewn into the plastic screen (21 cm above the bottom) was the only passage between the two compartments.

A porous pot (length, 22 cm; 8 cm outer and 6 cm inner diameter) in the home section served as a shelter. The stimulus section held an electric dipole, a feeder for rewards and a similar apparatus for 'punishment' with air bubbles (see Fig. 1). Reward (a bloodworm, *Chironomus*) and punishment (a few air bubbles) were

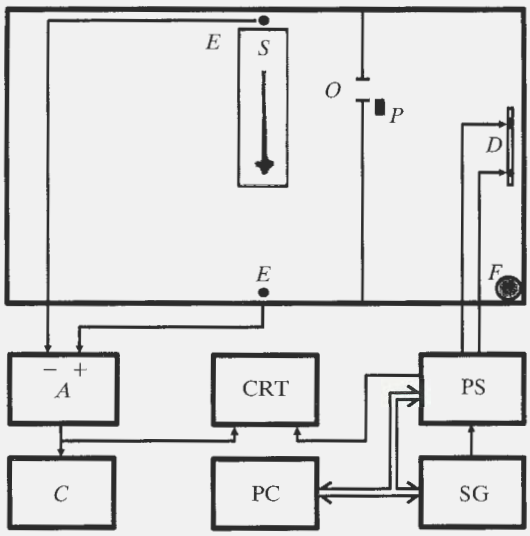

Fig. 1. Apparatus for testing *Eigenmannia*'s discrimination of stimuli varying in intensity or frequency. A plastic mesh screen separated the home compartment (with a porous pot as a shelter, *S*; left) from the stimulus compartment (right), which held an electric dipole (*D*), a feeder (*F*) and a device for punishing (*P*) the fish by injecting a few air bubbles, should it try to pass the opening (*O*) with the 'wrong' signal on the dipole. *E*, carbon rod electrodes for measuring the fish's discharge frequency; *A*, differential amplifier; *C*, electronic counter; CRT, oscilloscope. The stimulus chain included a sine wave generator (SG), a pulse shaper (PS) and a microcomputer (PC) controlling these devices *via* a digital interface. The bipolar (+/−) output of the pulse shaper was fed into the stimulus dipole (*D*), at an intensity 30 dB above threshold at that particular frequency (measured in the water).

delivered by a syringe-tube arrangement (one for each) operated manually from outside the tank. The bloodworms were injected into a small glass Petri dish in the observer's front right corner. Air bubbles were delivered at the passage connecting the two compartments, when fish tried to enter the stimulus section with the unrewarded signal on the electrodes. Simultaneously with receiving reward or punishment, the stimulus was turned off.

The electric dipole for stimulation consisted of two vertical carbon rods (diameter, 0.5 cm; length, 1.0 cm; separation, 7.8 cm) fixed on a horizontally oriented piece of transparent acrylic tubing (diameter, 1.3 cm; length, 12 cm), which also held the leads, sealed with silicone rubber. The dipole was oriented parallel to a fish's shelter, 2 cm from the short aquarium wall opposite the plastic mesh partition.

Absolute thresholds were determined by go/no-go conditioning of two fish. A fish resting in its shelter was presented for at least 60 s with the stimulus. After it had moved to the plastic screen and had remained there for more than 10 s without passing to the other side, the stimulus was turned off. A positive response was recorded when a fish passed the opening in the plastic screen in order to get its food reward (Fig. 1). A 50 % probability of responding was the threshold criterion. For each frequency tested, 16–33 trials were performed; the inter-trial interval varied from 2 to 4 min.

The sine wave signal was generated by a Hameg HM 8030–3 function generator (harmonic distortion, max. 0.04 dB); intensity was controlled by a Hewlett-Packard model 350D attenuator. The stimulus signal was made symmetrical (+/−) about zero by a small transformer (100 Hz–18 kHz) between the attenuator and the dipole. A fish's EOD frequency was measured with a Hameg 8021–3 electronic counter (±0.01 % at 500 Hz) after differential amplification (×100; 1 Hz–10 kHz). Stimulus intensities were measured next to the plastic screen (home section side), using a small silver ball dipole (ball diameter, 1 mm; separation, 10 mm) and a differential amplifier.

Thresholds were determined by the 'staircase' method; starting from subthreshold intensities, stimulus intensity was increased in 10 dB steps until a response was observed. By subsequently reducing the stimulus intensity by 5 dB, the threshold was determined within a 5 dB interval. By subsequently splitting the remaining interval in half (by increasing or lowering the stimulus intensity), thresholds were determined to ±1 dB.

To determine difference thresholds, both the electric apparatus and the training procedure were modified. Instead of a continuous sine wave, sine wave bursts were used (Fig. 2). The output of a programmable signal generator (Hewlett-Packard model 3314A, or 3325A for better than 1 Hz frequency resolution; frequency accuracy of sine waves ±0.2 % or ±0.0005 %, respectively) was fed into a programmable pulse shaper. These devices were controlled by a small computer (Hewlett-Packard model 85A) *via* a digital interface (HP-IB-Bus). Timed by the computer, the pulse shaper generated the rise and fall times (50 ms), as well as the holding (250 ms) and the silence (150 ms) times of the signal. The pulse shaper also

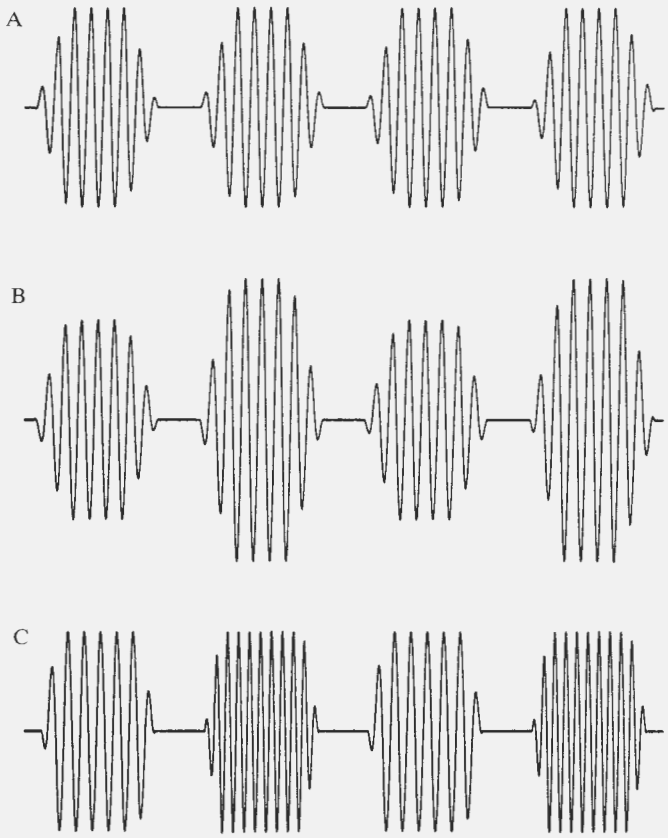

Fig. 2. Sine wave bursts as used for determining discrimination thresholds. (A) A series of sine wave bursts of constant intensity and frequency served as the negative, unrewarded stimulus (S−). (B) For studying intensity discrimination, the S+, or rewarded, stimulus consisted of constant-frequency sine wave bursts that alternated in intensity (by 3 dB in this example), with the lower intensity being the reference intensity (identical to the associated S− stimulus). (C) Frequency discrimination was studied using sine wave bursts of constant intensity, but alternating in frequency, as the S+ stimulus (the lower frequency was the reference frequency). For the illustration, but not for the experiments, very low frequencies (of 30 and 40 Hz) were chosen. All traces last 3.9 s.

served for programmed signal attenuation; it is described in more detail in Kramer and Weymann (1987). For the S+ stimulus, the sine wave bursts alternated either in intensity or in frequency; the basic intensity was +30 dB with reference to the absolute threshold at each frequency. The frequency of the S− signal was the lower of the two frequencies used for the S+ signal. The frequency of the S− stimulus was 1 Hz above a fish's resting EOD frequency, one of three lower frequencies or one of three higher frequencies (see Fig. 6). The stimulus frequency was unclamped, that is, constant throughout one presentation. Frequencies were chosen as a random sequence. The interval between stimuli was at least 2 min; a

stimulus was presented for up to 20 s. The smallest stimulus increments used were 0.25 dB for intensity and 0.25 Hz for frequency, near the EOD frequency of a particular fish. For other test frequencies, the smallest increments used were 1 dB and 1 Hz.

Discrimination conditioning was similar to the procedure detailed for absolute threshold estimation, except that a negative stimulus (S−) had to be discriminated from a positive, rewarded one (S+), and that the stimulus was turned off when a fish had shown no response for 20 s. Responses of the fish were recorded as (1) go/no-go responses (that is, 'yes' or 'no') and (2) the latency from stimulus onset to the fish passing the opening in the screen. Both methods yielded similar results. 50 % thresholds were estimated by interpolation from the curves for choice frequency *versus* stimulus increment (an example is shown in Fig. 5). The associated latencies for the S+ stimulus just above threshold were all significantly shorter than those for the S− stimulus (Mann–Whitney *U*-test, $P<0.05$, one-tailed; Sachs, 1984; see, for example, Fig. 4). The graphs in this paper all show the 50 % thresholds, although in some cases the thresholds determined by the latency method were smaller.

Results

Absolute thresholds

Absolute thresholds for sine wave stimuli of constant frequency were determined as a basis for the subsequent experiments focusing on intensity and frequency difference limits. Threshold frequency curves closely resembled those determined by Knudsen (1974), with lowest thresholds near EOD frequency (Fig. 3). However, near EOD frequency, Knudsen's thresholds are lower than ours (0.2–0.3 $\mu V_{p-p}\,cm^{-1}$ *versus* 1.75–2.60 $\mu V_{p-p}\,cm^{-1}$, respectively). Differences in methods may explain part of the variation (in Knudsen's study, the water conductivity of 500 $\mu S\,cm^{-1}$ was much higher; the threshold criterion of 70 % somewhat 'weaker' than ours, which would correspond to 75 % in his procedure; a measuring dipole of 5 cm, instead of 1 cm electrode separation: all these differences tend to lower the thresholds).

Thresholds rose with a mean 6.8 dB $octave^{-1}$ on the 'low', and 16.3 dB $octave^{-1}$ on the 'high' side of the 'best' frequency near a fish's EOD frequency (Fig. 3). The transition from 'no go' to 'go', or 0 % and 100 % responses, occurred within a narrow intensity range of only 2–4 dB at all frequencies.

Discrimination thresholds

Discrimination thresholds were determined by an equivalent of the 'pulsed sound technique', as used in auditory studies (see, for example, Fay, 1988). For the S+ stimulus, electric sine wave bursts alternated either in intensity (but not frequency) or in frequency (but not intensity; Fig. 2), while the S− stimulus was a constant series of bursts. Fish could thus compare the stimuli directly, and the

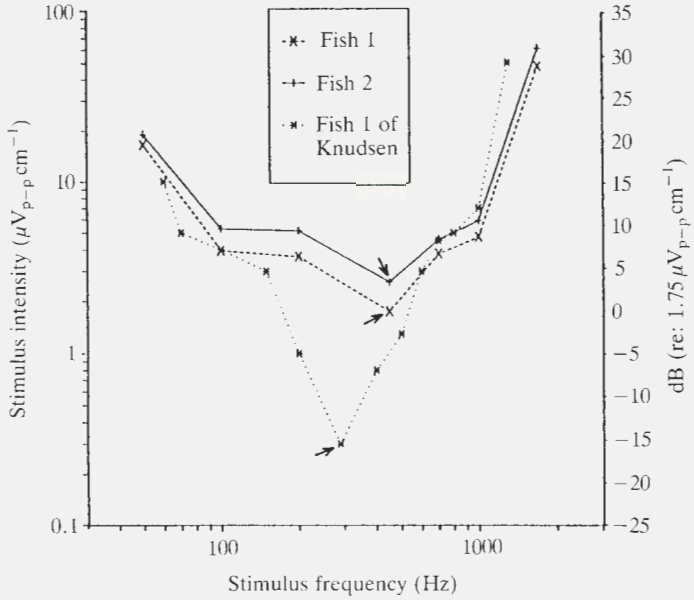

Fig. 3. *Eigenmannia*'s absolute detection thresholds of sine waves of steady frequency and intensity. Left ordinate, stimulus intensity in $\mu V_{p-p}\,cm^{-1}$; right ordinate, in dB with respect to the lowest threshold ($1.75\,\mu V_{p-p}\,cm^{-1}$) at 450 Hz, close to the fishes' discharge frequency). Dashed and solid lines, the two fish used in the present experiments; dotted line, Knudsen's (1974) result with one of his two fish, discharging at 290 Hz. Arrows, individual electric organ discharge (EOD) frequencies.

results did not depend on a precise geometrical relationship relative to the stimulus dipole. Lowest thresholds can be expected with this method.

Frequency discrimination

Responses were recorded as percentage correct choices, and also by testing for significantly shorter response latencies (delay from the stimulus onset to the fish passing the opening in the screen partition). Both methods yielded generally consistent results; that is, an S+ stimulus of the smallest frequency difference (Δf) that still evoked significantly shorter response latencies compared to the S− stimulus was normally associated with greater than 50 % of correct choices (the threshold criterion). Thresholds were determined from the percentage correct choices curves by linear interpolation between the two points that straddled the 50 % line (see Fig. 5).

For example, at a stimulus frequency 1 Hz below their individual discharge frequency, the smallest Δf that was still discriminated was 0.75 Hz in all three fish, as determined by significantly shorter latencies for the S+ compared to the S− stimulus (Fig. 4). The associated percentages of correct choices were 75 %, 80 % and 47 % (Fig. 5). Clearly, the unknown 'true' thresholds were lower than the test Δf of 0.75 Hz in the first two fish, while in the third this Δf may be assumed to be very close to the 'true' threshold. Therefore, thresholds were approximated by

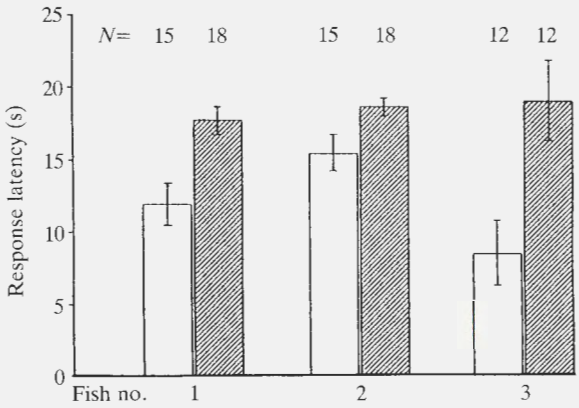

Fig. 4. Mean response latencies (s) ±S.E. of three *Eigenmannia* to a rewarded stimulus, S+ (open columns), and an unrewarded stimulus, S− (hatched columns). The S+ stimulus was a series of sine wave bursts, close to a fish's individual EOD frequency, that alternated in frequency by 0.75 Hz. The S− stimulus was identical to the S+ stimulus except that all sine wave bursts were of constant frequency (no alternation). The stimulation was stopped when a fish had shown no response after 20 s. An S+ stimulus with a frequency difference (Δf) of 0.75 Hz (as used here) was the smallest Δf that yielded significantly different results compared to the S− stimulus ($P<0.05$ in each pair of columns).

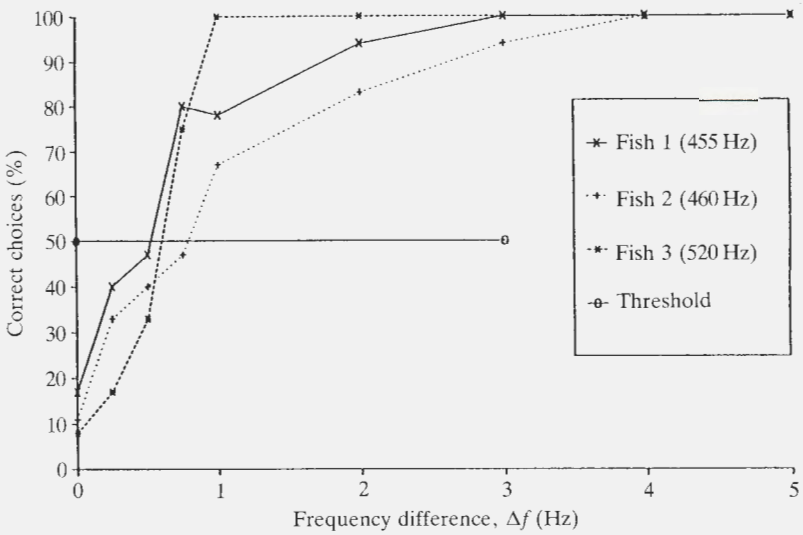

Fig. 5. Estimation of discrimination thresholds based on the percentage of correct choices (ordinate). Abscissa, frequency difference of the alternating sine wave bursts that distinguished the rewarded stimulus, S+, from the unrewarded stimulus, S− (consisting of constant-frequency sine wave bursts). The reference stimulus frequency was 1 Hz above a fish's individual resting frequency. Thresholds were determined as the intersection of the percentage correct choices curves with the 50 % line; difference thresholds were below 1 Hz in each fish.

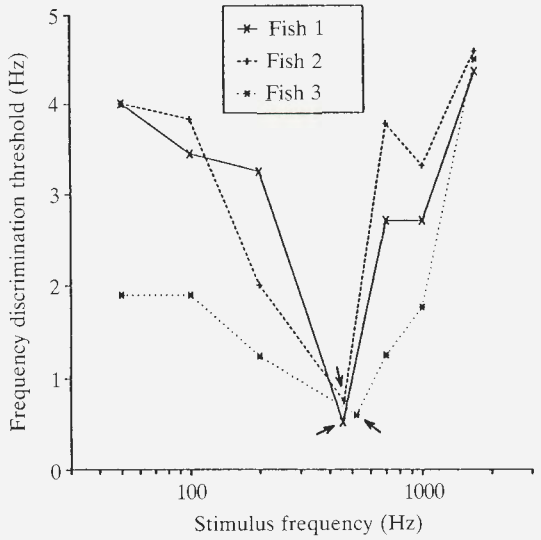

Fig. 6. Frequency discrimination thresholds as a function of the stimulus frequency. Note that the lowest discrimination thresholds were observed close to each fish's individual discharge frequency (arrows; three fish). Lowest thresholds ranged from 0.52 to 0.79 Hz.

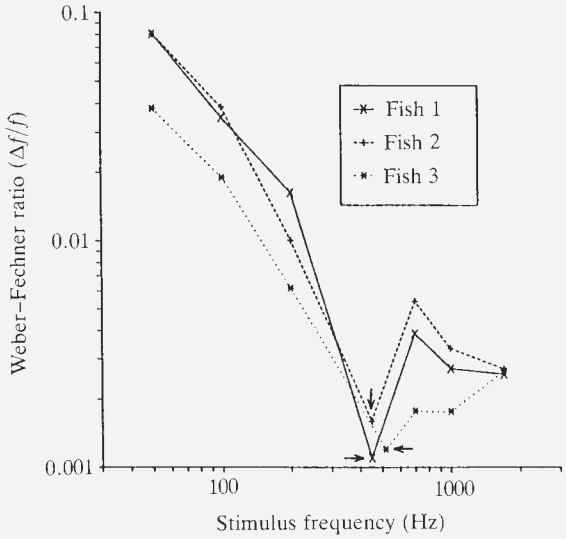

Fig. 7. Thresholds for relative frequency discrimination (Weber–Fechner ratio, $\Delta f/f$) over stimulus frequency. Lowest values (best relative frequency discrimination) were observed close to the three fishes' individual discharge frequencies (arrows), while there was a dramatic rise at lower frequencies, much more marked than at higher frequencies. Best relative frequency discrimination values were 0.11–0.17% of the stimulus frequency.

interpolation for 50 % correct choices, as shown in Fig. 5. This yielded thresholds of 0.52 and 0.60 Hz for the first two fish, while the third fish's apparent threshold rose slightly to 0.79 Hz by this procedure.

Thus, Δf thresholds ranged from 0.52 to 0.79 Hz at stimulus frequencies close to the three test fishes' individual discharge frequencies. Frequency discrimination was best at these frequencies, and rose for both lower and higher frequencies (Fig. 6). On the 'low' side of a fish's EOD frequency, discrimination thresholds rose at a rate of up to 1 Hz octave^{-1}, while this value was up to 3 Hz octave^{-1} on the 'high' side. At 50 Hz stimulus frequency, Δf thresholds were still $\leq$4 Hz; at 1700 Hz, below 5 Hz.

The Weber–Fechner ratio expresses these Δf values as a fraction of the stimulus frequency. For example, close to the three test fishes' individual EOD frequencies, Δf thresholds were 0.11 %, 0.12 % and 0.17 % of the stimulus frequency. The ratio deteriorated considerably at low frequencies (up to 8 % in two fish and less than 4 % in the third, at 50 Hz stimulus frequency), while it remained remarkably low (that is, good frequency discrimination) at frequencies higher than the EOD frequency (less than 0.6 % throughout the whole 'high-frequency' range tested; Fig. 7).

Intensity discrimination

The same procedures as those detailed above for frequency discrimination were

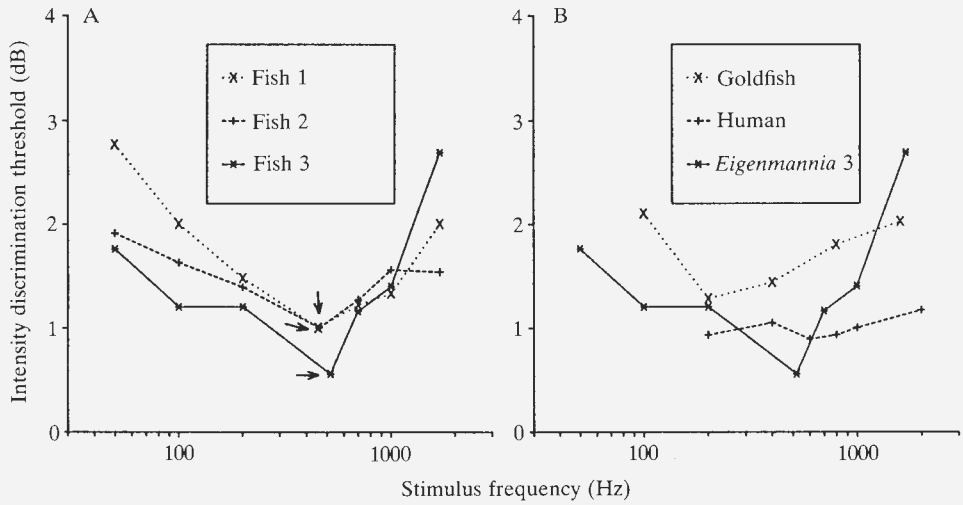

Fig. 8. Intensity discrimination thresholds for electrical, compared with auditory, stimuli, as a function of stimulus frequency. Ordinate, difference between sine wave bursts alternating in intensity. (A) Note that, in *Eigenmannia*, lowest electrosensory discrimination thresholds were observed close to each fish's individual discharge frequency (arrows; three fish). Lowest thresholds ranged from 0.56 to 1 dB. (B) Thresholds for auditory intensity discrimination in the goldfish (Fay, 1989) and human (Jesteadt *et al.* 1977) compared with the electrosensory thresholds of our most sensitive *Eigenmannia* (from A).

used for the investigation of the fishes' intensity discrimination, except that the sine wave stimuli used in a trial were of constant frequency throughout, for all seven test frequencies.

Not only frequency discrimination but also intensity discrimination were best close to a fish's individual discharge frequency: thresholds for an intensity difference (ΔI) were 1 dB in two fish, and 0.56 dB in the third fish (a mean ΔI of 0.83 dB; Fig. 8A). Intensity discrimination deteriorated only slowly at both lower and higher stimulus frequencies than the EOD frequency. On the 'low' side, ΔI thresholds rose at a rate of less than 1 dB octave^{-1}, while on the 'high' side, this rate was below 2 dB octave^{-1}.

Discussion

This is the first study of electrosensory difference thresholds for frequency and intensity (excluding a study of pulse-rate discrimination in a pulse-discharging fish, *Pollimyrus isidori*; Kramer and Heinrich, 1990). Before discussing the main issues of the present paper, *Eigenmannia*'s absolute threshold for sine waves should be briefly considered.

Absolute electrosensory threshold

As already observed by Knudsen (1974), and also seen in the present paper (Fig. 3), the absolute threshold of trained *Eigenmannia* for sine wave stimuli of constant frequency and amplitude was lowest close to their own individual discharge frequencies, with thresholds increasing steeply at both lower and higher frequencies. A V-shaped curve was also found for the tuning curves of individual electroreceptors (especially for the T-units; Scheich *et al.*, 1973; Hopkins, 1976).

Thresholds for the spontaneous jamming avoidance response, evoked close to a fish's individual discharge frequency, are generally within the same range: about 10 μV cm^{-1} (Watanabe and Takeda, 1963; Larimer and MacDonald, 1968); 0.5 μV_{p-p} cm^{-1} (Bullock *et al.* 1972) and about 2 μV_{p-p} cm^{-1} (Kramer, 1985). These results were obtained using widely differing water conductivities and techniques. The present thresholds for a conditioned go response (1.75–2.6 μV_{p-p} cm^{-1}; Fig. 3) correspond best to the JAR threshold of Kramer (1985), determined at the same water conductivity (100 μS cm^{-1}). This remarkable coincidence of thresholds for totally different behaviors, determined by totally different techniques, shows that the JAR is indeed evoked by stimuli as weak as the absolute sensory threshold.

Electrosensory frequency and intensity discrimination

Not only did *Eigenmannia* discriminate electric sine waves of different frequencies, but its frequency resolution was particularly high. *Eigenmannia* discriminated differences as low as 0.52 Hz (0.60 and 0.79 Hz in two other fish), or 0.11 % of the stimulus frequency (0.12 % and 0.17 %, respectively). Close to a fish's discharge frequency, discrimination thresholds were lowest; they rose at

rates of up to 1 Hz octave^{-1} and up to 3 Hz octave^{-1} at lower and higher frequencies, respectively.

Eigenmannia's best frequency resolution, as determined in the present study, compares well with that determined for the JAR, using the polarity reversal of the response in juveniles as a criterion ('not better than ±0.3 Hz', that is, 0.6 Hz; Kramer, 1987). This suggests that the same sensory mechanism is involved (that is, the analysis of the amplitude and phase modulations of the beat patterns, resulting from the superposition of the stimulus field with the fish's own electric field; Scheich, 1977; Heiligenberg, 1989). However, in those fish that do show the response (Kramer, 1987), the JAR resembles a reflex-like behavior, and there frequency discrimination need not be involved. By contrast, our trained fish had to show that they had detected a frequency difference by their overt behavior.

Eigenmannia also showed acute intensity discrimination when stimulated with sine wave bursts of alternating intensity (Figs 2, 8). The discrimination threshold close to a fish's individual EOD frequency was as low as 0.56 dB (1 dB in two other fish). The JAR also shows strong intensity-dependence, which is proportional to the logarithm of the stimulus intensity (Watanabe and Takeda, 1963; Kramer, 1985). (The slope of this relationship is, however, highly variable among individuals; Kramer, 1987.) The resolution of *Eigenmannia*'s intensity discrimination was best at stimulus frequencies close to its own individual discharge frequency; difference thresholds rose at both lower and higher frequencies by less than 1 dB octave^{-1} and less than 2 dB octave^{-1}, respectively (Fig. 8A).

Comparison of discrimination thresholds with natural signals or signal modulations

The difference thresholds, as determined in the present paper, may be compared with signals or signal modulations occurring in object detection and communication, the two functions of the electrosensory-motor system.

In active object detection, an *Eigenmannia* discriminating an intensity change of its own EOD of 0.56 dB, or 7 %, would be able to detect a distance change of an object (metal cylinder) 4 mm in diameter by 0.32 mm at a distance from the fish's skin of 10 mm (calculated according to Bastian, 1986; Fig. 3B).

A frequency difference threshold of 0.5 Hz appears to be well adapted to *Eigenmannia*'s habit of communicating by frequency modulations (although waveform recognition is also involved; see Introduction). The standard deviation of *Eigenmannia*'s normal resting frequency fluctuations over 1 min is below ±0.125 Hz (N=1200 EODs sampled over 1 min; Kramer, 1987). This fluctuation should be below the detection threshold. By contrast, frequency modulations displayed during social signalling (see review by Hagedorn, 1986) are all greater than the difference threshold. For example, 'long rises' consist of a smooth increase in frequency over several seconds, by 2.5–40 Hz; 'short rises' consist of a 20–40 Hz change over 1–2 s; 'frequency drops' of about 20 Hz are followed by an increase to the resting frequency over about 45 s; 'warbles' consist of frequency modulations of up to 20 Hz over about 45 s (etc.).

Electrosensory versus *mechanosensory discrimination thresholds*

Difference thresholds are known for other acoustico-lateral senses in lower vertebrates – for water surface waves and in audition. The surface-feeding topminnow (*Aplocheilus lineatus*) detects and localizes prey by water surface waves. Its frequency resolution is 10 % (2 Hz at 20 Hz stimulus frequency; see review by Bleckmann, 1988). The clawed frog's (*Xenopus laevis*) best frequency discrimination of water surface waves is 4 %; it is found at 14 Hz stimulus frequency (Elepfandt *et al.* 1985).

A pulse-discharging mormyrid fish, *Pollimyrus isidori*, discriminates a 2 % variation in the rate of electric pulses at 20 pulses s^{-1} and a 3 % variation at 10 pulses s^{-1} (similar to the human stimulated with sound clicks; Kramer and Heinrich, 1990). For technical or physical reasons, these studies could not use an equivalent of the 'pulsed sound technique', as employed in the present paper; therefore, these studies represent thresholds for 'absolute pitch' (no direct comparison of frequencies or rates). Lower thresholds would be expected should the 'pulsed sound technique' be used. This technique was, however, applied in studies of the goldfish's hearing; the best frequency resolution of 3.5 % of the stimulus frequency was found at 500 Hz (40 dB sensation level; Jacobs and Tavolga, 1968) or 3.7 % at 400 Hz (35 dB sensation level; Fay, 1970).

This short list shows that *Eigenmannia*'s electrosensory frequency difference thresholds given in the present study, although determined at a comparatively low sensation level, are without parallel among the other acoustico-lateral senses of lower vertebrates. Even the most sensitive of the higher vertebrates with a cochlea (see review by Fay, 1988), like the European starling (*Sturnus vulgaris*, at 60 dB sensation level; Kuhn *et al.* 1980) or the human (at 40 dB sensation level; Wier *et al.* 1977), cannot better *Eigenmannia*'s electrosensory frequency discrimination of 0.11–0.17 %, being 0.4 % and 0.16 %, respectively, at these species' respective 'best' frequencies for sound signals (however, Zwicker, 1982, gives only 0.7 % for the human at 60 dB sensation level, a value perhaps more typical for most members of our species). To our knowledge, it is only in a bat that we find an even better frequency resolution than that of *Eigenmannia*: 0.05 % in the greater horseshoe bat *Rhinolophus ferrumequinum*, apparently at 80 dB sensation level (Heilmann-Rudolf, 1984). However, this superior auditory acuity is present only within an extremely narrow range (±1 kHz) about the sonar frequency of 83 kHz, because of the bat's specialized cochlea (Bruns, 1976; Vater *et al.* 1985). Behavioral absolute thresholds increase at up to 170 dB $octave^{-1}$ with increasing difference from the sonar frequency (Long and Schnitzler, 1975).

A comparison of electrosensory and auditory frequency discrimination thresholds, including a lower vertebrate without and a higher vertebrate with a cochlea, in relation to stimulus frequency is shown in Fig. 9. All three species display a loss of frequency resolution below 500 Hz, or, in *Eigenmannia*, below its discharge frequency; this loss is especially rapid in *Eigenmannia*. At its 'best' frequency, however, the lowest threshold is found in *Eigenmannia*, and it remains remarkably low at high frequencies. At their respective 'best' frequencies, the

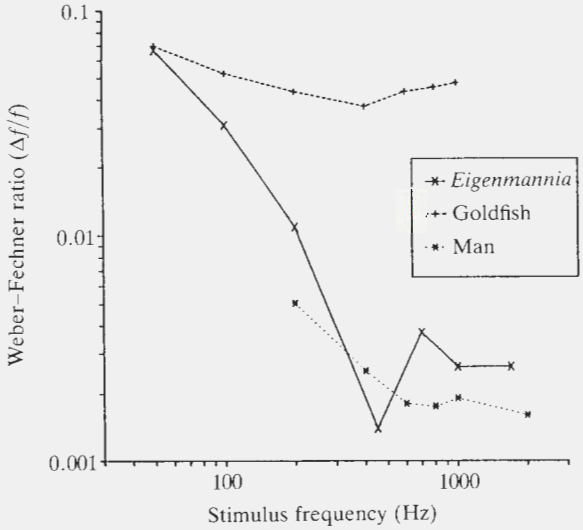

Fig. 9. Comparison of electrosensory and auditory frequency discrimination in three vertebrates (*Eigenmannia*, electrosensory; $N=3$). Relative frequency discrimination is expressed as Weber–Fechner ratios ($\Delta f/f$) as a function of stimulus frequency (Hz) at similar sensation levels (*Eigenmannia*, 30 dB; goldfish, 35 dB; human, 40 dB). Note that the lowest difference threshold occurs in *Eigenmannia*, at a stimulus frequency close to its discharge frequency of 450 Hz, although no specialized transducer, like man's cochlea, functions ahead of the receptor cells. *Eigenmannia*'s electrosensory frequency resolution shows, however, a dramatic decline at lower frequencies compared to the frequency of best resolution; at higher frequencies, its frequency resolution remains remarkably high (goldfish, Fay, 1970; human, Wier *et al.* 1977).

goldfish should detect the slight mismatch of two pure tones that are separated by a little more than a quarter tone on the musical scale; a human, 1/77 tone (only 1/17 tone according to the value given by Zwicker, 1982); and *Eigenmannia*, about 1/100 'tone' (from 1/72 to 1/111, depending on the individual).

The relative constancy of electrosensory thresholds (expressed as Weber–Fechner ratios) at higher frequencies relative to a fish's discharge frequency reminds one that sine waves of subharmonic frequencies (that is, half, one-third, etc. of the EOD frequency) do not evoke a JAR, whereas for higher harmonics the effective frequency difference remains constant (Bullock *et al.* 1972; Kramer, 1985).

More controversial than its auditory frequency discrimination is the goldfish's ability to discriminate small changes in level between two pure tone bursts of the same frequency, with the lowest values ranging widely from about 1.3 dB at 55 dB sensation level (Fay, 1989) to 4 dB at 40 dB sensation level (Jacobs and Tavolga, 1967) in the range 200–300 Hz (Fig. 8B). The goldfish's intensity discrimination thresholds show little dependence on frequency, being only 2.2 dB from 100 to 1600 Hz (on average 0.7 dB higher at the lower sensation level of 35 dB; Fay, 1989). At only 30 dB sensation level, *Eigenmannia*'s thresholds for electrosensory

intensity discrimination were equal to or below 2 dB from 50 to 1700 Hz, with the exceptions of fish no. 1 at 50 Hz and fish no. 3 at 1700 Hz (thresholds below 3 dB; Fig. 8A). In all three fish, there was a sensitivity maximum close to a fish's individual discharge frequency, with fish no. 3 presenting the very low threshold of 0.52 dB (or 7 % change). Even for the human, one of the most sensitive vertebrate species, not only for sound frequency but also for sound intensity discrimination, the lowest threshold is greater (0.89 dB at 600 Hz and 40 dB sensation level, Fig. 8B; Jesteadt *et al.* 1977).

Mechanism of electrosensory frequency discrimination

What is so special in *Eigenmannia*'s electrosensory system that such superior frequency and intensity discrimination is achieved? All other species mentioned so far, except the bat and *Eigenmannia*, must deal with unpredictable signals received from the environment, varying over several orders of magnitude in frequency and intensity. *Eigenmannia* and the bats emit their own energy at stable amplitudes and frequencies. Therefore, receptor sensitivity on the one hand, and amplitude and frequency of the 'test' signal on the other, are coadapted. Receptors are stimulated at their 'best' frequency, and information about the environment is encoded as modulations of the self-generated signal. In contrast to the horseshoe bat, which extracts information about the environment by successive comparison of its emitted sonar pulse with the received echo (which is weak and variable in intensity, but of similar frequency to the emitted sound pulse), *Eigenmannia* performs a simultaneous analysis of its own EOD superimposed on another electrostatic field (beat analysis), using receptors stimulated at their 'best' frequency and best working range. *Eigenmannia*'s EOD as a 'carrier' signal is modulated in amplitude and phase by the extraneous electric field, according to that signal's frequency difference, amplitude and waveform (see, for example, Kramer and Otto, 1991). *Eigenmannia*'s tuberous receptors, P- and T-receptors, transmit this amplitude and phase modulation to higher brain centers where the frequency difference is probably computed (see reviews by Heiligenberg, 1989; Carr, 1990). We have now shown that *Eigenmannia* detects a small change in the frequency difference between its own EOD and an extraneous sine wave.

In contrast to the bat, *Eigenmannia* does not need exceptionally sharp tuning of its electrosensory periphery; hence, it incurs neither the considerable cost in frequency band transmitted nor the waveform deformation that is associated with sharp tuning (the waveform carries socially relevant information; see Introduction; Kramer and Otto, 1991). Instead, *Eigenmannia* carries out a time-domain analysis of the beat pattern which is repeated at a much lower frequency than the signal to be analyzed (the difference frequency between the EOD and the extraneous signal). The difference frequency increases at both lower and higher frequencies relative to a fish's discharge frequency; as does the frequency discrimination threshold.

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